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The annual cycle in populations of earthworms (Lumbricidae Oligochaeta) in three types of oak-hornbeam of the Niepołomicka Forest

II. Dynamics of population numbers, biomass and age structure

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With 3 figures

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1. Prefatory note

It is generally accepted that where earthworms are abundant they have significant roles in the process of litter decomposition (Satchell 1967). Hence studies on the population ecology of earthworms were initiated as part of the programme on nutrient cycling and pollutants in the Niepołomicka Forest (Grodziński, Weiner & Maycock 1984).

2. Study area, materials and methods

The study was carried out in oak-hornbeam stands in the northern part of the Niepołomicka Forest (Ferchmin & Medwecka-Kornaś 1976, Grodzińska 1984). Three sites were chosen for the study: site I was situated in a "low" oak-hornbeam stand (Tilio-Carpinetum stachyetosum), site II in a medium moist category of "high" oak-hornbeam stands (Tilio-Carpinetum typicum, variant with *Aegopodium podagraria*), site III in the relatively dry variant of "high" oak-hornbeam (Tilio-Carpinetum typicum, variant with *Convallaria maialis* and *Poa nemoralis*). The sites differed in the species composition of the herb layer and relative moisture content (table 1). Sampling was carried out monthly from July 1977 to July 1978. A combination of methods was used (Zajonc 1970); at each site eight soil samples were collected, each 25 cm × 25 cm to a depth of 20 cm, and sorted by hand, and then a dilute formalin solution was used to expel earthworms from deeper soil layers. The earthworms were rinsed, dried on blotting-paper and weighed; the weighed individuals were then preserved in 4% formalin (Rożen 1982).

The results are expressed as means ± standard deviations. Differences in the numbers of earthworms between three sites were tested using Analysis of Variance.

3. Results

3.1. *Total population densities*

The numbers of earthworms found in successive months at each site are expressed both in terms of the annual mean and of month to month population dynamics.

The highest mean annual density was recorded in the moist, "high" oak-hornbeam, where it came to 174.7 ± 133.9 ind. × m^{-2} it was intermediate in the "low" oak-hornbeam — 142.8 ± 102.1 ind. × m^{-2}, and lowest — only 65.5 ± 61.5 ind. × m^{-2} — in the dry, "high" oak-hornbeam. These densities fluctuated from month to month, reflecting changes in activity, reproduction, or mortality (table 2).

In the "low" oak-hornbeam, the highest numbers for the autumn period were recorded in September (164 ± 86.7 ind. × m^{-2}). No marked decrease in numbers was observed till December, the lowest number being recorded in February (14 ± 10.2 ind. × m^{-2}). The

Table 1. Annual changes in earthworm numbers (ind. $\times m^{-2}$) in three oak-hornbeams of the Niepołomicka Forest

		Jul	Aug	Sep	Oct	Nov	Dec
Low oak-hornbeam	N	98.0	160.0	164.0	160.0	150.0	104.0
	±SD	±81.8	± 94.0	± 86.7	± 52.6	± 82.9	± 61.1
	Ad	42.0	40.0	68.0	50.0	34.0	16.0
	Imm	56.0	120.0	96.0	110.0	116.0	88.0
Moist, high oak-gornbeam	N	190.0	210.0	180.0	172.0	88.0	76.0
	±SD	±131.5	±161.3	± 87.0	± 81.9	± 35.2	± 49.6
	Ad	56.0	64.0	40.0	40.0	16.0	6.0
	Imm	134.0	146.0	140.0	132.0	72.0	70.0
Dry, high oak-hornbeam	N	70.0	116.0	52.0	44.0	22.0	28.0
	±SD	± 81.9	± 69.9	± 31.7	± 29.3	± 28.3	± 28.0
	Ad	28.0	30.0	24.0	14.0	4.0	2.0
	Imm	42.0	86.0	28.0	30.0	18.0	26.0

		Jan	Feb	Mar	Apr	May	Jun	Jul
Low oak-hornbeam	N	76.0	14.0	96.0	144.0	214.0	246.0	230.0
	±SD	±71.4	±10.2	± 45.3	± 64.4	±111.2	±131.7	±133.3
	Ad	10.0	4.0	8.0	24.0	46.0	74.0	86.0
	Imm	66.0	10.0	88.0	120.0	168.0	172.0	144.0
Moist, high oak-hornbeam	N	82.0	28.0	102.0	314.0	244.0	328.0	258.0
	±SD	±36.6	±26.7	± 84.6	± 86.7	±141.3	±137.9	±158.1
	Ad	12.0	6.0	14.0	66.0	90.0	54.0	84.0
	Imm	70.0	22.0	88.0	248.0	154.0	274.0	174.0
Dry, high oak-hornbeam	N	44.0	—	30.0	90.0	80.0	80.0	130.0
	±SD	±55.2	—	± 21.8	± 57.9	± 42.4	± 79.8	± 80.7
	Ad	2.0	—	4.0	28.0	41.0	44.0	90.0
	Imm	42.0	—	26.0	62.0	39.0	36.0	40.0

N — toal numbers, Ad — adults, Imm — immatures

numbers rose gradually in the spring, reaching a maximum of 246 ± 131.7 ind. $\times m^{-2}$ in June.

Changes in earthworm numbers followed a similar pattern in the moist, "high" oak-hornbeam. Here, the summer-autumn peak occurred in August (210 ± 161.3 ind. $\times m^{-2}$); a drop was recorded in December (76 ± 49.6 ind. $\times m^{-2}$). After winter the highest numbers were found in June (328 ± 137.9 ind. $\times m^{-2}$).

Similar seasonal patterns of earthworm densities were recorded in the dry variant of "high" oak-hornbeam site with higher populations in August (116 ± 69.9 ind. $\times m^{-2}$) and declining in September to 52 ± 31.7 ind. $\times m^{-2}$. The minimum count would have probably been in February, as at the other two sites (it was impossible to take samples that month). In the spring-summer period of 1978, the highest earthworm count at this site was found in July (130 ± 90.7 ind. $\times m^{-2}$).

3.2. *Species population*

3.2.1. General

It is important to have some knowledge not only of the overall population dynamics during the year, but also of the dynamics of the numbers of particular species. *Dendrobaena rubida*, *Fitzyngeria platyura v. montana* and *Eiseniella tetraedra* will not be considered here, because their numbers were too small to make valid inference possible.

Table 2. Annual changes in earthworm biomass ($gm_h \times m^{-2}$) in three oak-hornbeams of the Niepołomicka Forest

		Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Low oak-hornbeam	B	32.0	29.7	39.2	49.4	49.1	16.0	10.7	2.3	11.4	36.4	53.3	69.9	80.5
	±SD	±31.4	±15.0	±20.5	±19.0	±49.3	±11.2	±13.4	±4.0	± 8.8	±23.2	±36.8	39.2	48.3
	Ad	22.2	12.4	28.5	28.6	32.1	7.1	3.4	1.9	3.8	12.6	25.0	29.8	37.7
	Imm	9.6	14.3	9.4	17.9	15.3	7.7	5.3	0.4	6.5	14.6	23.5	31.7	23.0
Moist, high oak-hornbeam	B	3o.7	33.2	34.6	33.8	12.3	4.7	7.4	2.0	10.2	57.5	72.8	75.3	65.3
	±SD	±25.9	±24.6	±19.7	±17.2	± 5.1	± 3.4	± 3.4	±3.2	±10.6	±16.0	±47.2	±32.0	±43.5
	Ad	15.9	16.2	14.1	11.2	3.8	0.9	3.3	0.8	3.0	21.1	42.7	18.8	24.2
	Imm	18.3	16.2	19.4	19.1	7.4	3.6	2.9	1.1	1.5	31.5	23.5	48.3	30.4
Dry, high oak-hornbeam	B	13.2	21.9	12.7	7.1	2.0	2.0	3.2	—	3.4	21.2	25.9	29.9	41.2
	±SD	±13.4	±17.3	±12.2	± 5.8	± 2.2	± 2.2	± 3.7	—	± 2.9	±11.4	±13.9	±25.4	±25.4
	Ad	7.1	7.6	8.4	3.8	0.3	0.3	1.1	—	0.8	14.0	15.4	19.0	30.6
	Imm	5.6	13.1	3.2	3.1	1.5	1.6	2.1	—	2.4	6.3	6.0	8.0	7.5

B — total biomass, Ad — adults, Imm — immatures

Depending on the type of habitat they occupy, earthworms can be classified into three ecological groups: epigées — litter dwellers, endogées — horizontal burrowers, and anecique — deep burrowers (Bouché 1970, cit. after Phillipson *et al.* 1976). Only the first two groups are considered here, because there is only one species of the third group in the Niepołomicka Forest *(Fitzyngeria platyura v. montana)*.

3.2.2. Endogees

This group is represented in the Niepołomicka Forest by *Aporrectodea caliginosa*, *Aporrectodea rosea* and *Octolasion lacteum*. All these species show the same pattern of population dynamics during the year — a single peak abundance during the summer months with a decline in the winter (fig. 1). The similarity in population trends can be ascribed to the similar habitats which they occupy.

3.2.3. Epigees

Dendrobaena octaedra: no clear pattern was observed in the fluctuation of numbers of this species. Although the highest numbers were found in the spring and summer months, no clear decline took place in winter months (fig. 2).

3.2.4. Intermediate

Lumbricus rubellus: numbers of this species declined in the winter months followed by a substantial increase in spring (fig. 2).

3.3. *Biomass*

A similar mean biomass was found in both "low" and moist "high" oak-hornbeam ("low" oak-hornbeam — 32.6 ± 29.5 g hygro-mass $\times m^{-2}$, moist "high" oak-hornbeam — 31.1 ± 28.6 $gm_h \times m^{-2}$. A lower biomass of only 14.1 ± 13.0 $gm_h \times m^{-2}$ was found in the dry "high" oak-hornbeam (table 3).

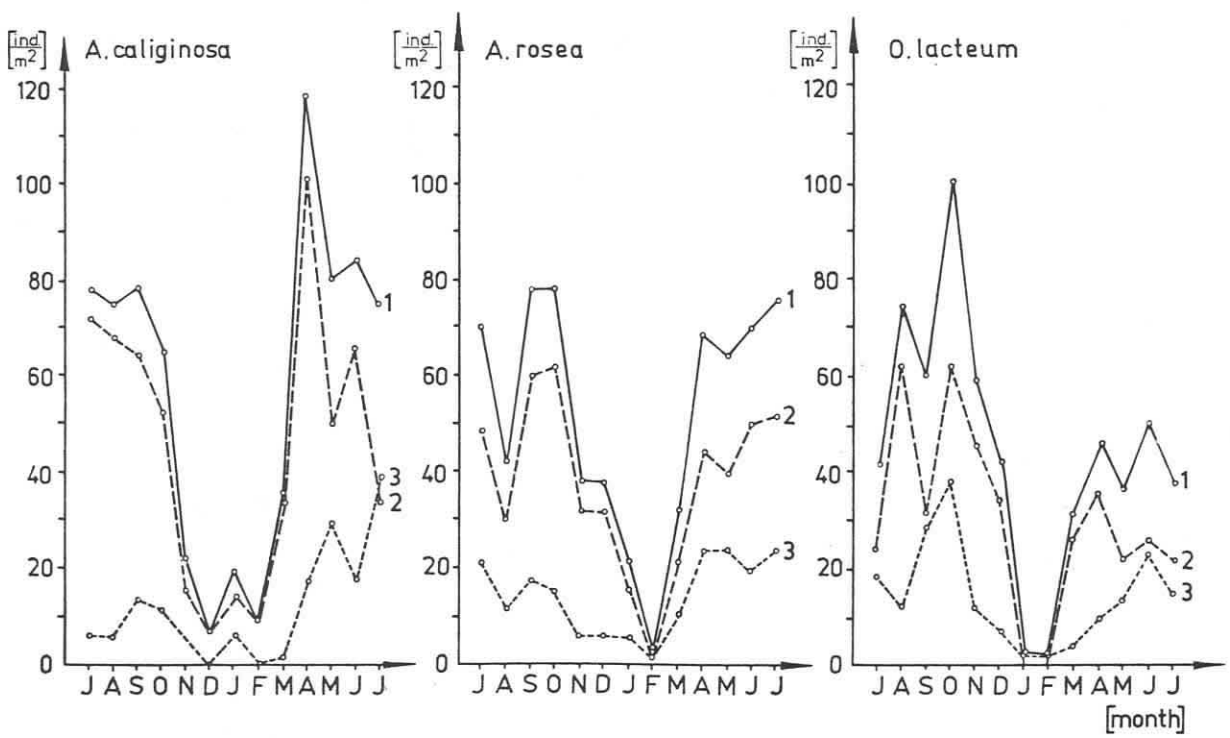

Fig. 1. Annual changes in earthworm abundance (ind. $\times m^{-2}$) for particular species and age classes in the oak-hornbeam of the Niepołomicka Forest. 1 — total number, 2 — immature individuals, 3 — adult individuals.

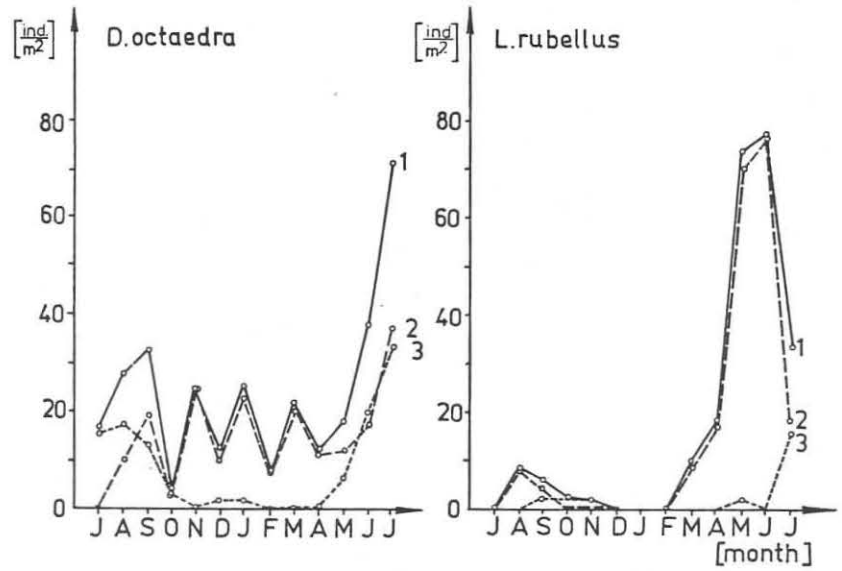

Fig. 2. Annual changes in earthworm abundance (ind. $\times$ m^{-2}) for particular species and age classes in the oak-hornbeam of the Niepołomicka Forest. 1 — total number, 2 — immature individuals, 3 — adult individuals.

Table 3. Ratios of adult to immature earthworm numbers in three oak-hornbeams of the Niepołomicka Foest

Species Site	*Aporretodea caliginosa*	*Aporretodea rosea*	*Octolasion lacteum*	*Dendrobaena octaedra*	*Dendrobaena rubida*	*Lumbricus rubellus*	*Fitzyngeria platyura*	*Eiseniella tetraedra*
Low oak-hornbeam	1:2.3	1:3.6	1:2.1	1:1.8	1:0.1	1:8.7	1:19	1:3.5
Moist, high oak-hornbeam	1:3.8	1:2.6	1:1.2	1:1.7	1:1.5	1:14.5	—	—
Dry, high oak-hornbeam	1:1.7	1:2.4	1:0.5	1:1.8	1:0.1	1:2.5	—	—

The biomass changes during the year followed trends in population densities. Before winter, the highest biomass in the "low" oak-horn-beam was observed in October, in July 1977 in the moist "high" oak-hornbeam, and in August in the dry "high" oak-hornbeam. The lowest earthworm biomass was recorded in February in the moist "high" oak-hornbeam and "low" oak-hornbeam, and in December in the dry "high" oak-hornbeam (no samples were taken at this site in February).

Endogee species constitute a similar fraction of the total biomass as of the total number. This however was not the case for *Dendrobaena octaedra*. In the dry "high" oak-hornbeam this species dominated in terms of its numbers (33.2%), while it was only fourth in terms of its biomass (17.3%). *Fitzyngeria platyura v. montana* constituted a high proportion of the biomass — 8.4%, while by numbers it was only 2.2% *Eiseniella tetraedra* constituted 2.9% of the total number, but only 0.5% of the biomass.

For the endogees, i.e. *Aporrectodea caliginosa*, *A. rosea* and *Octolasion lacteum*, the seasonal biomass dynamics presents a similar pattern to that of numbers, namely a high autumn, spring and summer biomass, and a decline in winter (fig. 2).

In the case of *D. octaedra* (epigée) the graphs of population and biomass changes during the year differ. While no regular annual changes of numbers can be seen (fig. 2), the biomass of this species drops in winter and rises in the spring (fig. 3).

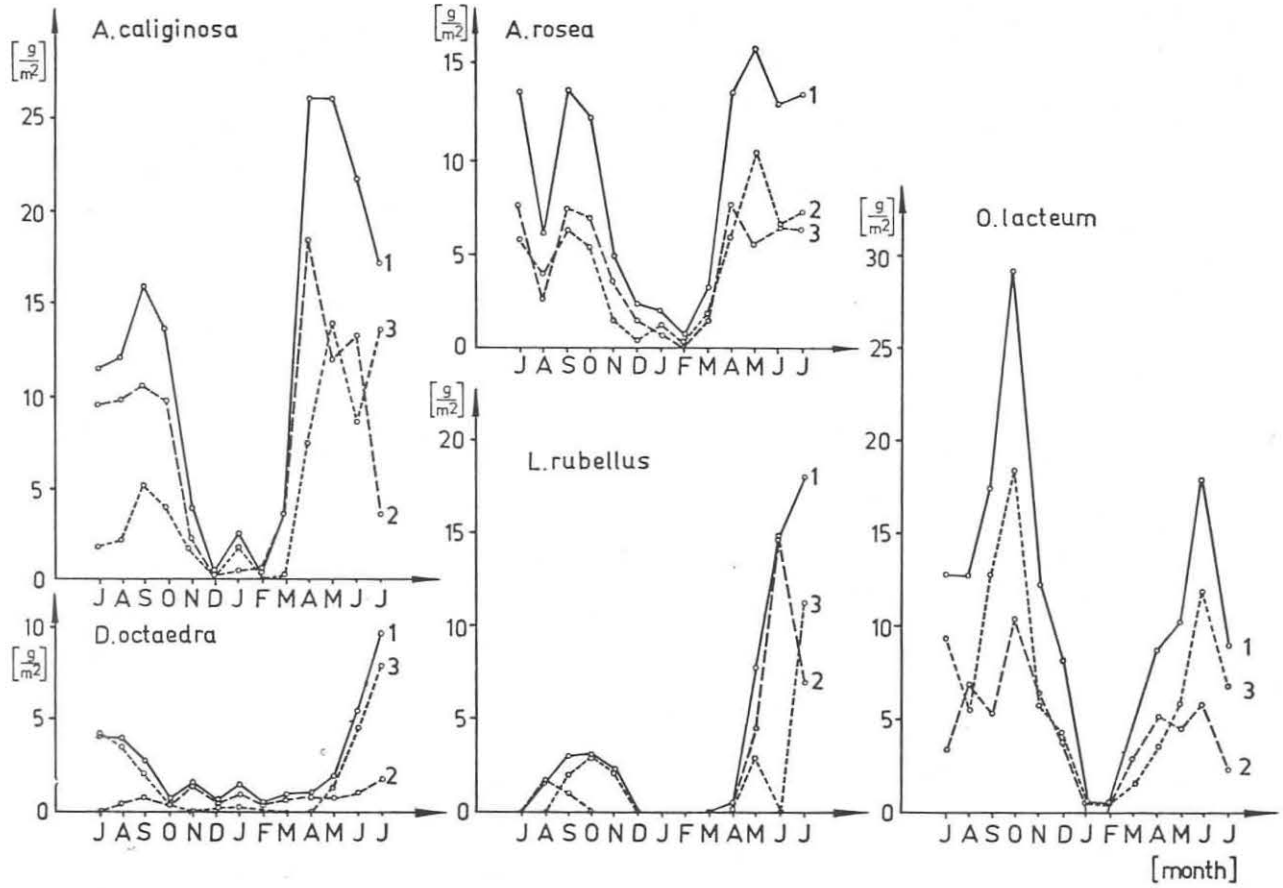

Fig. 3. Annual changes in earthworm biomass ($gm_n \times m^{-2}$) for particular species and age classes in the oak-hornbeam of the Niepołomicka Forest. 1 — total biomass, 2 — immature individuals, 3 — adult individuals. The total biomass does not equal the sum of the biomasses of adult and immature individuals.

3.4. *Age structure*

In this paper only two classes have been defined: immatures and adults. Young individuals, which have not yet developed a *clitellum* or any *tuberculae pubertatis*, have been classified as immatures.

The mean yearly ratio of adult to immature individuals was 1 : 2.7 in the "low" oak-hornbeam, 1 : 3.1 in the moist "high" oak-hornbeam and 1 : 1.5 in the dry "high" oak-hornbeam. The ratios of adults to immatures for each species are presented in table 4.

In both "high" and "low" oak-hornbeam, the numbers of adults were lower than those of immatures the whole year round (table 2). The autumn decline and the spring increase in the number of adults was slower than for the immature individuals. Only in the dry "high" oak-hornbeam was this pattern different. Although the number of young individuals was higher from summer till winter 1977, adults dominated from spring 1978. This may have been caused by the freezing of some of the cocoons and an increased mortality among young individuals.

As a rule in annual cycles of the ratios of adults to immatures, the number of adults is below 50% of the overall count for any one species. Here, the number of adults of a given species was inversely proportional to the total number, so that the proportion of adults was higher at sites of low density.

This was not the case for *D. octaedra*, where adults constitued a high proportion of the total (over 50%) in spring and summer months, and the lowest proportion in winter.

It is evident from the graphs for numbers of adult and immature endogée that in the annual cycle the winter decline in adult numbers started early and was slow. The rise in numbers followed a similar pattern in spring. In the case of immatures, the winter drop in numbers came later, but was much more rapid and abrupt. In the spring (March—April)

the number of immatures increased rapidly, and subsequently remained at a similar level or declined slightly (fig. 1).

For *D. octaedra*, adults showed the same kind of population density dynamics as endogees. No seasonal changes in numbers of immature individuals were observed. Winter counts of immatures of this species were high at all three sites (fig. 2). This might have been the result of a greater tolerance of this species to cold, combined with a limited capacity for vertical movement.

Lumbricus rubellus exhibits single-peak population dynamics for both adults and immatures similar to the endogées (fig. 2).

The total biomass, both of adult and immature individuals, exhibited clear annual dynamics. In the "low" oak-hornbeam the biomass of adults was higher or approximately equal to that of the immatures, while in 1977 a lower adult biomass was characteristic of the dry "high" oak-hornbeam. In the summer of 1978, the biomass of adults was clearly higher there (table 3).

The biomass of individual species followed single-peak dynamics at all three sites during the year, with a peak in the spring summer period (figs. 3, 4). Adult biomass was higher for *A. caliginosa* ("low" oak-hornbeam), *O. lacteum* (all sites) and *D. octaedra* (all sites, except in winter months).

For *A. caliginosa* the biomass of immature individuals exceeded that of the adults in moist "high" oak-hornbeam. In *A. rosea* in both the "low" and "high" moist oak-hornbeam, the biomass per square metre was similar for adults and immatures. For *A. caliginosa* and *A. rosea* in the dry "high" oak-hornbeam the ratio of adult to immature biomass varied during the year. The biomass of young individuals was higher before winter, the opposite was true after winter. In *L. rubellus* the ratio was variable at all sites.

4. Discussion

Oak-hornbeam is not a uniform type of forest association, and exhibits considerable structural variety in relation to soil moisture and fertility. The three kinds of oak-hornbeam forests investigated in this study differed in the species composition of the herb layer and in moisture, *p*H and clay content of the soil. These differences influence both numbers and species composition of earthworm populations. Therefore, in order to describe the earthworm population of the Niepołomicka Forest as a whole, simultaneous studies were carried out in these three main woodland habitat types. Differences in numbers of earthworms between the three sites were tested using Analysis of Variance. The "low", "high" moist and "high" dry oak-hornbeam sites differed highly significantly ($F = 9.175$, $p < 0.001$).

In a six months study (June—December) of earthworms in the Kampinoska Forest, NAKAMURA (1981) found a low mean number of only 23 ind. $\times m^{-2}$. The number of earthworms reported for the oak-hornbeam in the Niepołomicka Forest in November is also low — 20.8 ind. $\times m^{-2}$ (NAKAMURA 1981). In the present study, the November population densities were as follows: 150 ind. $\times m^{-2}$ for the "low" oak-hornbeam, 88 ind. $\times m^{-2}$ for the moist "high" oak-hornbeam, and 22 ind. $\times m^{-2}$ for the dry "high" oak-hornbeam.

In a study completed in oak-hornbeam in Slovakia, Zajonc (1971) found a mean yearly population density of 105 ind. $\times m^{-2}$ (below that in the "low" oak-hornbeam and the moist "high" oak-hornbeam), yet the biomass was considerably higher (98 $gm_h \times m^{-2}$).

In a year-long study of English beech forest, PHILLIPSON *et al.* (1976) found a mean yearly population density of 138.2 ind. $\times m^{-2}$ (1971/72) and biomass of 51.28 g $\times m^{-2}$ (PHILLIPSON *et al.* 1978). In a Swedish beech forest (NORDSTRÖM & RUNDGREN 1973) the biomass was 15.4—33.3 $gm_h \times m^{-2}$) (recalculated), at a much lower mean yearly population density (67—90 ind. $\times m^{-2}$).

The relatively low earthworm biomass at fairly high numbers, found in the Niepołomicka Forest, is due to a species composition different from that in the other forests discussed here. The only large species, *Fitzyngeria platyura v. montana*, was found exclusively

in "low" oak-hornbeam where it comprised only 2.2 % of the population. In the other forests mentioned here there are some larger species not present in the Niepołomicka Forest, such as *Octolasion cyaneum*, *Allolobophora longa* and *Lumbricus terrestris*.

Neither earthworm numbers nor their biomass are constant parameters. Their changes during the year can be explained by fluctuations in activity, reproduction and mortality. This leads to difficulties in comparing the results of field studies carried out at different times of the year. When considering the dynamics of earthworm population numbers, one can speak of either single peak dynamics with a drop in numbers occurring only in winter, or of double peak dynamics with a pronounced drop in numbers in winter, and a smaller decline in summer (ZAJONC 1970). Double peak dynamics are typical of soils which are more exposed to atmospheric conditions — especially in open areas. In forest ecosystems, the microclimate at soil level is much more stable. Therefore, in these ecosystems single peak population dynamics with a decline occurring in winter are often the rule. In the sites studied in the Niepołomicka Forest, a few dormant individuals were found, but only in summer 1977. In the summer of 1978 all the earthworms were active, which was due to the higher soil moisture (higher precipitation). The population dynamics observed in Niepołomicka Forest were of the one peak type. In a mixed forest in Hungary, a very high proportion of inactive earthworms was found between July and October and also in February (ZICSI 1959). In the forests of southern Sweden, a summer drop in earthworm activity was also recorded, associated with higher soil temperature and lower moisture (NORDSTRÖM 1975).

When inspecting the seasonal density changes, it was found that earthworm populations of different species behaved differently. The population densities of all endogées, i.e. *A. caliginosa*, *A. rosea* and *O. lacteum*, were high in spring, summer, and autumn and very low in winter. The epigées, *D. octaedra* and *E. tetraedra* (probably also *D. rubida* — NORDSTRÖM 1975) behave in quite a different way with no clear winter decline in numbers. From these data it can be deduced that epigées have a wider range of tolerance to temperature. This is hardly surprising, since epigées, being litter dwellers, with a limited capacity for burrowing, are more likely to be influenced by ambient weather conditions. These observations are in agreement with earlier data from Swedish forests (NORDSTRÖM 1975), where *D. octaedra* was active at a soil temperature of approximately 0 °C. This is not the case for *L. rubellus*. A drop in its numbers occurred in winter in the "low" and dry "high" oak-hornbeam, but this decrease was not clear in the moist "high" oak-hornbeam. These results suggest species dynamics of an intermediate type, between endogées and epigées, although NORDSTRÖM (1975) has reported that the activity patterns of the genera *Lumbricus* and *Dendrobaena* are similar.

The oak-hornbeam sites studied varied in the ratios of adults to immatures, which were: 1 : 2.7 ("low" oak-hornbeam), 1 : 3.1 (moist "high" oak-hornbeam) and 1 : 1.5 (dry "high" oak-hornbeam).

In the oak-hornbeam of Bab (ZAJONC 1971) the ratio was 1 : 2.2 i.e. in the same sort of range as in the Niepołomicka Forest. This ratio was considerably lower for grassland ecosystems. On Carpathian meadows in Czechoslovakia (ZAJONC 1970) it was 1 : 1.03, and 1 : 0.9 for meadow in Hungary (ZISCI 1959). These data show that the ratio of adult to immature individuals is fairly high in forest ecosystems, reflecting conditions which are favourable to earthworm hatching and development.

The seasonal dynamics of earthworm numbers in an annual cycle show that the number of adult individuals of all species fall earlier on in the year and rise again later than the number of immatures do. For *D. octaedra*, the population density dynamics are quite different for young and adult individuals. Adult numbers drop in winter, while for the immature individuals no clear changes are apparent at any time, most important of all there is no winter decrease in numbers. A different tolerance to cold for different age groups may account for this. Observations have shown that the sites studied differed in species composition, numbers, biomass and also in age structure.

Earthworms play an important part in the decomposition of litter, and thus in the cycling of organic matter and energy flow in ecosystems. In deciduous forests, such as the

Niepołomicka Forest, they also transport appreciable quantities of organic matter deeper into the soil. The role of earthworms in the ecosystem depends on their number, biomass and metabolism (PHILLIPSON *et al.* 1978). The higher the earthworm population density, the more quickly litter is broken down. In the oak-hornbeam studied, litter decomposition is more rapid in the "low" and the moist "high" oak-hornbeam than in the dry "high" oak-hornbeam. Earthworms have much less impact on litter decomposition in the southern of the Niepołomicka Forest, which is a pine forest complex; in coniferous forests earthworm numbers are low, and small species predominate (*D. octaedra* in the Niepołomicka Forest). For this reason, litter decomposition is much slower there than in the oak-hornbeams of the Niepołomicka Forest (KARKANIS 1975).

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ROŻEN, A., 1988. The annual cycle in populations of earthworms (Lumbricidae, Oligochaeta) in three types of oak-hornbeam of the Niepołomicka Forest. Pedobiologia **31**, 169—178.

Ecological studies on earthworms were conducted in three variants of oak-hornbeam woods in the Niepołomicka Forest: "low" oak-hornbeam (Tilio-Carpinetum stachyetosum), moist "high" oak-hornbeam (Tilio-Carpinetum typicum, variant with *Aegopodium podagraria*), dry "high" oak-hornbeam (Tilio-Carpinetum typicum with *Convallaria maialis* and *Poa nemoralis*). From July 1977 to July 1978 earthworms were sampled every month. The highest mean annual density was recorded in the moist "high" oak-hornbeam — 174.7 ind. $\times$ m^{-2}, it was intermediate in the "low" oak-hornbeam — 142.8 ind. $\times$ m^{-2}, and lowest — only 65.5 ind. $\times$ m^{-2} in the dry "high" oak-hornbeam. These densities fluctuated from month to month reflecting changes in activity, reproduction or mortality. All species belonging to the endogée group *(A. caliginosa*, *A. rosea* and *O. lacteum)* show the same pattern of population dynamics during the year — the highest numbers in the spring and summer, and the lowest in winter. No clear pattern was observed in fluctuation of numbers of *D. octaedra*. A similar biomass was found in both low and moist "high" oak-hornbeam (32.6 gm$_h$ $\times$ m^{-2} and 31.1 g m $\times$ m^{-2}). A lower biomass of only 14.1 gm$_h$ $\times$ m^{-2} was found in the dry "high" oak-hornbeam. The mean yearly ratio of adult to immature individuals was 1: 2.7 in the "low" oak-hornbeam; 1: 3.1 in the moist "high" oak-hornbeam; 1: 1.5 in the dry "high" oak-hornbeam. In the annual cycle the winter decline in adult numbers started early and was slow. The rise in numbers followed a similar pattern in spring. In the case of immatures, the winter drop in numbers came later but was more rapid and abrupt. In the spring the number of immatures increased rapidly and subsequently remained at assimilar level or declined slightly.

Key words: soil fauna, earthworms, numbers, biomass, age structure.